A MORPHOLOGICAL ANALYSIS OF ROW NUMBER IN MAIZE

EDGAR ANDERSON
Missouri Botanical Garden,
AND WILLIAM L. BROWN
Pioneer Hi-Bred Corn Company, Johnston, Iowa

The kernels of an ear of maize are usually set in longitudinal rows of from 8 to 30 or more. Certain genetic stocks, and an occasional ear in open-pollinated varieties, may have only 4 rows. For numbers much above 30, the kernels are so crowded that the rowing is obscure; various irregularities may modify or conceal the row pattern (Weatherwax, 1916, 1917), but in most of the varieties of *Zea Mays* the kernels over a good portion of the ear are arranged in definite and usually conspicuous rows. In nearly all varieties the row number is even, since the kernels arise from paired spikelets which are themselves disposed in regular rows (Collins, 1919).

The history of row number is apparently complex. Both in South America and in the southwestern United States archaeological investigation has demonstrated that the earliest varieties had 12 or 14 rows (Bird and Anderson, in press), and Bird's recent excavations indicate that this condition persisted unchanged for a long period. Both in South America and in the southwest 8- and 10-rowed varieties appeared at a later date (Carter and Anderson, 1945). Another type of change in row number has been associated with the dent corns of Mexico. Since at least the times of the Toltecs, row numbers of 16 and above have been characteristic of central Mexico (Anderson, 1946), and it is apparently chiefly from that center that they have been so widely spread around the world as to characterize many of the world's centers of commercial corn production.

Since the early days of studies upon inheritance in *Zea Mays* (Emerson and East, 1913) it has been apparent that the genetic basis for differences in row number is complex. Extensive and careful studies were carried on by the late R. A. Emerson and his students and collaborators for several decades. While he made a number of preliminary and informal reports his results in different crosses were rather contradictory and have not yet been formally published. Lindstrom (1929, 1931) observed linkage between genes for row number and genes for pericarp color.

The morphological bases for differences in row number are difficult to study upon the ear itself, an organ so modified that its exact relation to other grass inflorescences is still a subject for research and so highly vascularized that such research is technically difficult. Accordingly, for the past decade, we have carried on a comprehensive survey of variation in both the ear *and* the tassel (the male and female inflorescences). As Bonnett's (1940) developmental studies have clearly shown, these two inflorescences are scarcely distinguishable morphologically in their early stages but beyond a certain point the ear becomes progressively harder and thicker, the tassel progressively more lax and expanded. From modern

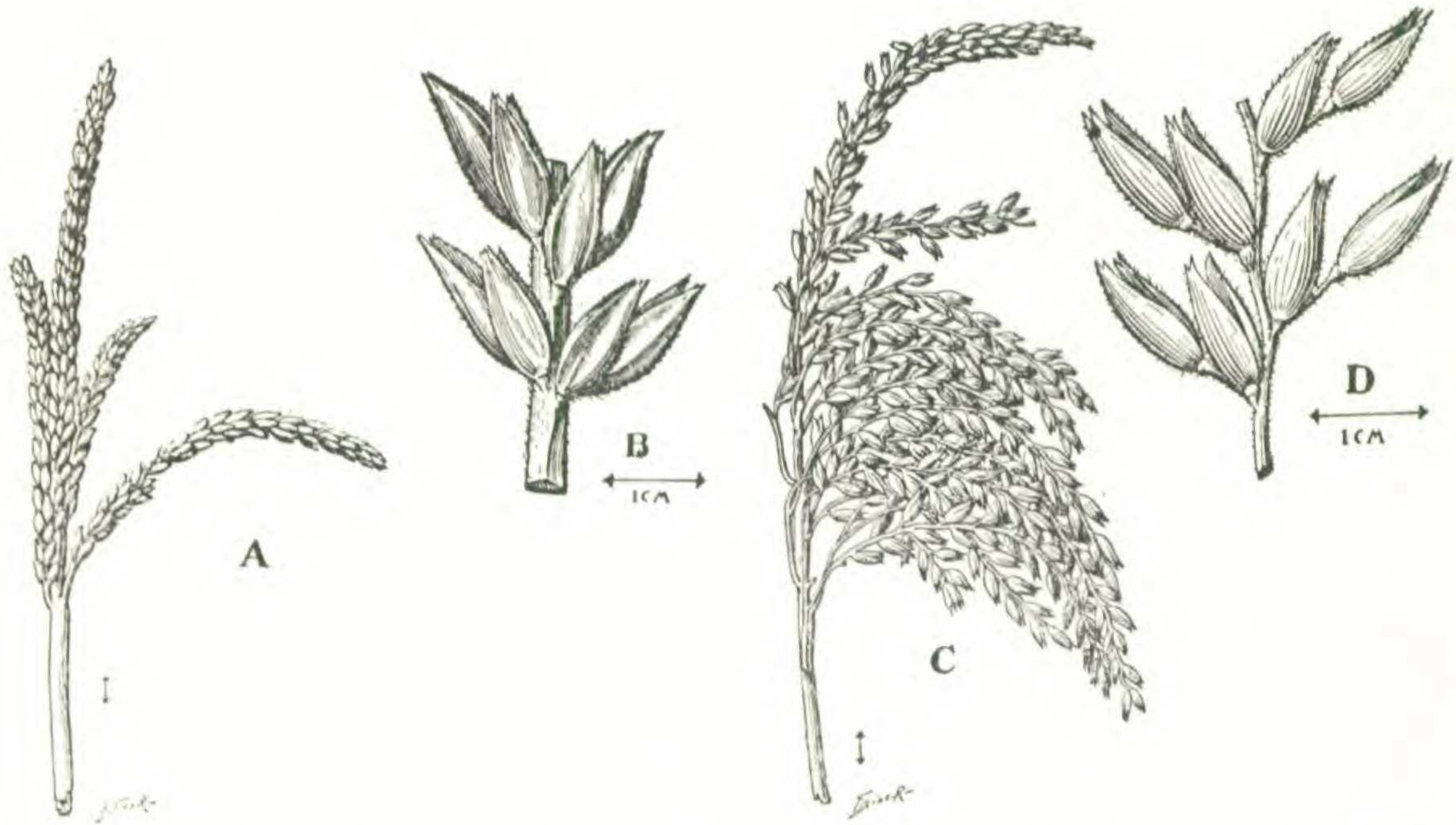

Fig. 1. Two extreme tassel types from an inbred plot. *A* and *C* show the general habit of the tassel. A few branches have been removed from *C* as indicated in the drawing, to reveal the structure of the tassel. *B* and *D* show equivalent portions of the lowest tassel branch from *A* and *C*. The arrow under the figures is 1 cm. in length. Condensation in *B* is 2.0, in *D*, 1.0.

genetic theory we know that the germinal differences between various types of ears will also be operating in the tassels of those same plants. Since the tassel is an expanded and relatively unmodified organ, changes which are difficult to determine and equally difficult to interpret when viewed only in the ear are easier to score and simpler to understand when studied in the tassel. Therefore, though this paper is primarily an attempt to analyze variation in the ear, we must first consider the morphology of the tassel with reference to its pattern of variation.

Though the tassel (like all other parts of the corn plant) varies greatly from one strain to another, its basic plan is singularly uniform. It is composed of a central axis with a varying number of secondary branches, terminated by a dense portion which has generally been referred to as the central spike. The secondary branches may themselves be branched, particularly the lower ones, and in some kinds of maize there may even be branching of the fourth and fifth order.

The fundamental unit of the tassel is the spikelet, technically a condensed raceme. It is about a centimeter long and has two chaffy basal glumes which cover and conceal the remainder of the spikelet except for a short period during anthesis. In *Zea* the spikelets of the tassel are almost universally borne in pairs, one of which is practically sessile, the other being noticeably (and oftentimes conspicuously) pedicellate (fig. 1). This condition characterizes not only *Zea* but nearly all of the genera in the two tribes of grasses (Maydeae and Andropogoneae) with which this genus is obviously most closely related.

In modern maize one of the most conspicuous variables in tassel structure is the arrangement of the spikelet pairs. In the wild grasses related to maize these arise one pair at each node, and in South America and in the Orient there are wide areas in which all the varieties of maize are so characterized. In the maize of central Mexico, however, this fundamental pattern has been so greatly altered as to be almost unrecognizable in its extreme manifestations. Since it was apparently from this center that most of the dent corns of commerce were ultimately derived, these same anomalies, in a somewhat diluted form, are to be found in all the areas of commercial corn production where dent corns play a dominant role.

Superficially, the Mexican dents (and associated rice popcorns) are characterized by compact, clubby tassels, densely set with spikelets. This condensation is equally true of the central spike, and of all the secondary and tertiary branches. When the spikelet arrangement on the secondary branches is examined in detail, it is evident that the dense effect is due to a kind of fasciation or telescoping of successive nodes. This telescoping may be of various intensities. In some commercial United States varieties it affects only a portion of the nodes. In such varieties the majority of the nodes will bear a single pair of spikelets, but a few may have two or more pairs. The most extreme manifestations of this tendency are seen in such kinds of maize as the short-eared many-rowed dents from central Mexico to which Anderson and Cutler (1942) have given the name of Mexican Pyramidal, and in the closely related rice popcorns such as Japanese Hull-less. In these varieties there may be no normal nodes along the whole length of the tassel branch, and the average number of spikelet pairs per apparent node may be four or five. (We say apparent node since there are various reasons for believing that the node number itself has not been primarily affected and that the peculiarities of these kinds of maize are due to a telescoping of successive internodes so that what seems to be but a single node with several pairs of spikelets is in reality a succession of nodes virtually on top of each other, each with its own pair of spikelets.)

This telescoping of the inflorescence has been designated as "condensation" (Anderson, 1944). Its effect can be seen throughout the tassel and it might conceivably be measured in the central spike, or on all or on one of the secondary tassel branches. Experience has shown that the most consistent results are obtained when it is scored on the lowermost secondary branch. (When, as in certain inbred strains, the lowest tassel branch is manifestly malformed, the next branch above is chosen for scoring.) Condensation is scored by recording for the central portion of the branch the ratio between the number of pairs of spikelets and the number of apparent nodes. (For precise directions see Anderson, 1944). This ratio runs from 1.0 in the uncondensed varieties of South America and of the Orient, to 4.0 and higher in Mexican dents and in certain inbred lines which resemble them.

As soon as the phenomenon of condensation had been recognized it was obvious that there was a close connection between condensation of the tassel and high row numbers of the ear. All maize varieties with row numbers of 16 or above were, without exception, found to exhibit condensation in the tassel. Eight-rowed varieties, without exception, were found to have no condensation. By utilizing inbred lines to minimize the effects of environmental variation it was possible to demonstrate that the over-all relation between row number in the ear and condensation of the tassel is so exact that it may be expressed in a mathematical equation. If we let C represent the condensation ratio, and R the number of rows on the ear, then these two variables are related in the following way:

$$R = 10C.$$

The relationship has been tested with a wide variety of material,—United States open-pollinated varieties, inbred lines derived from these varieties, Mexican varieties, Guatemalan varieties, popcorns, sweet corns, etc. The exactness of the correlation depends upon the variability of the stock which is being examined. If, as in the original investigation, one grows twenty or more plants of various inbred lines under optimum conditions, choosing a characteristic tassel from each inbred line, and a well-developed ear, then the correlation will be very high. There are a very few inbreds in which condensation of the tassel is not accompanied by a corresponding increase in row number, but they are very much in the minority as fig. 2 demonstrates. If open-pollinated maize is grown, two or three plants to a hill, and then the condensation of each tassel is correlated with the row number of each ear, the correlation is quite naturally less exact, but it is still clearly demonstrable.

In the commercial dent varieties of the United States there is an interesting variation in this correlation which has a logical basis. In Mexico the relationship between condensation and row number approaches a simple straight-line (Wellhausen, Roberts and Lenz). In United States dents the relationships between these two variables is curvilinear as shown in fig. 2. In other words, in North American maize a tassel may indicate an exceedingly high degree of condensation, yet the row numbers will be only in the lower 20's instead of in the 30's. This is probably due to the intense selection for ears of 18 to 22 rows which took place for several decades under the influence of the corn shows. The corn-show ideal called for an ear of 18 to 22 rows, but discriminated highly against ears with higher row numbers. During this period modifying genes which would have held down the expression of high condensation in the ear would have been at a selective advantage. The differences between scatter diagrams for tassel condensation vs. row number in Mexico and in the United States suggest that such modifiers are common in United States varieties. Further evidence for such modifiers was obtained from crosses between the two common inbred lines, WF-9 and 38-11, with Japanese Hull-less popcorn, a variety with a very high row number and extreme condensation. F-2's of 125 plants each were grown and scored for row number

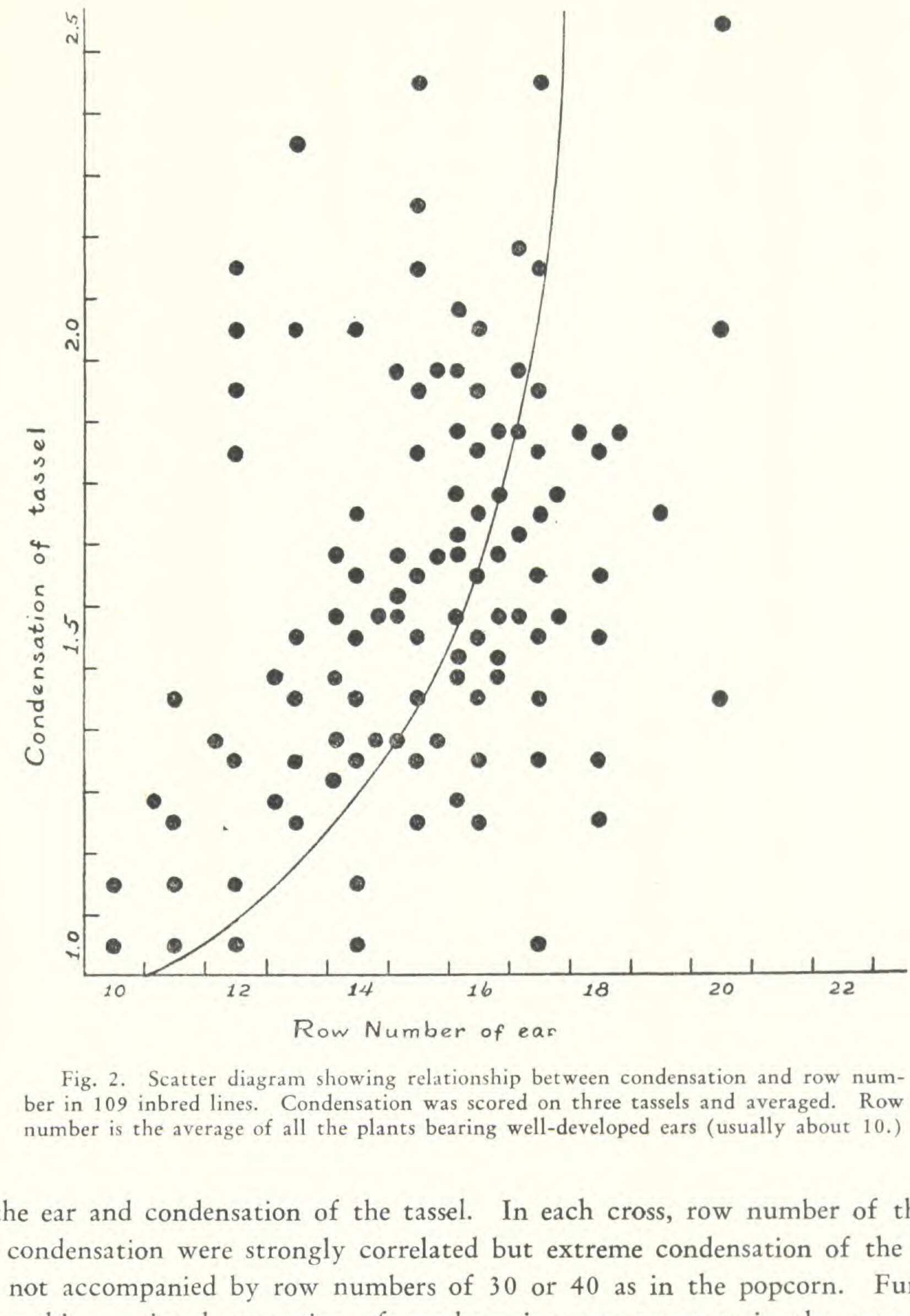

Fig. 2. Scatter diagram showing relationship between condensation and row number in 109 inbred lines. Condensation was scored on three tassels and averaged. Row number is the average of all the plants bearing well-developed ears (usually about 10.)

of the ear and condensation of the tassel. In each cross, row number of the ear and condensation were strongly correlated but extreme condensation of the tassel was not accompanied by row numbers of 30 or 40 as in the popcorn. Furthermore, this restricted expression of condensation was stronger in the cross with WF-9 than in that with 38-11. It was even greater in an F-2 between 38-11 and WF-9 than in the crosses with Japanese Hull-less. These results indicate that corn-belt maize does carry modifying genes which hold down the expression of condensation in the ear and that there are more such modifiers in WF-9 than in 38-11.

If condensation of the tassel is to be used as a precise indication of row-number potentiality, it must, however, be carefully determined. Since the first paper

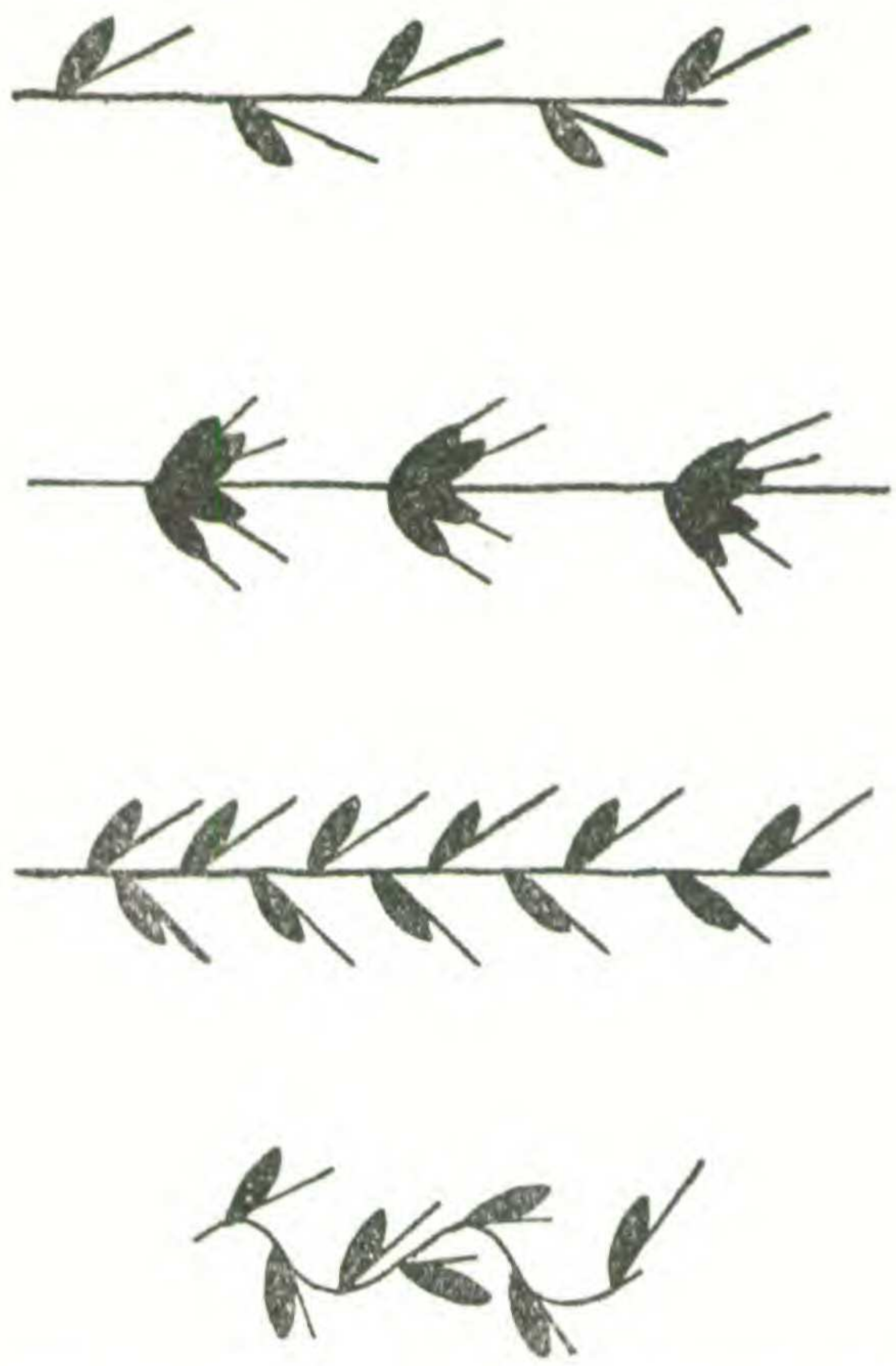

Fig. 3. Diagram showing various arrangements of the spikelet pairs on secondary branches of the tassel. In all four diagrams only the pedicel of the pedicellate spikelet is shown. From above to below: normal; highly condensed; short internodes; spiralled axis. Although the lower two produce thick-looking tassels which are superficially similar to those with condensation, their thickness is due to fundamentally different phenomena and has no effect upon row number.

(Anderson, 1944) on this subject some workers have attempted to lessen the tedium of tassel examination node by node. They have instead measured the density of the tassel in some such way as number of spikelets per centimeter of length. Though condensation does indeed produce a dense tassel, there are numerous other variables which may produce dense tassels without affecting the row number, as, for instance, short internodes or a spiraled axis (fig. 3). While it is true that after one understands the effects of condensation he can often estimate the row potentialities by merely glancing at a tassel in the field, it is equally true that in any precise investigation of the phenomenon it must be accurately determined according to the original directions.

Another abnormality of the inflorescence which affects row number has been described as "multiplication" by Cutler (1946). It apparently causes the bifurcation of the spikelet at a very early developmental stage so that two spikelets are produced instead of one. A high degree of multiplication is difficult to distinguish from a high degree of condensation, but lower grades are readily distinguishable in the tassel. In condensation the spikelet pairs tend to be regular, but successive pairs are arranged practically on top of each other. In multiplication the arrangement is normal but either or both of the spikelets within the pair is doubled. The effects are also different on the ear. Condensation produces ears in which the row rumber has been increased but in which the rowing is still regular. Multiplication adds additional kernels in a more or less crowded irregular fashion until the regularity of the rowing is no longer apparent. Extreme multiplication is rare in the United States and in Mexico, common in certain kinds of Guatemalan maize, particularly the yellow flints of the mountains, and is common in parts of South America. Its expression is most readily studied in what would otherwise be an 8-rowed variety. With a little multiplication there are occasional diamond-shaped kernels squeezed in between the regular rows. This is a common condition in flints of the northeastern United States. With a further development of the phenomenon there are so many of these extra kernels that the ear is divided into four quadrants, each representing two original rows. Within each of these quadrants the rowing is difficult or impossible to make out. With still further multiplication, the entire ear is so crowded with kernels that it can no longer be considered to possess a definite row number.

In the earliest stages of our investigation Dr. G. Ledyard Stebbins pointed out, from his wide knowledge of the Gramineae, that such phenomena as condensation and multiplication represent obvious teratological variations which have been selected under cultivation because they increase the row number and hence the productivity of the crop. Continued study has confirmed the soundness of his judgment. Nothing like either multiplication or condensation is characteristic of any of the wild-growing Gramineae. Furthermore, the extreme manifestations of condensation, such as are seen in certain inbreds or in an occasional ear from an open-pollinated variety of dent corn, are clearly fasciated. In the prehistoric remains of maize from the American southwest these fasciated extremes seem to have been more frequent when highly condensed varieties were first introduced into that area than they now are. This would suggest that the condensed varieties have gradually accumulated a set of modifiers which allow condensation to increase row number but tend to prevent the production of extreme, fasciated ears.

Therefore, if we are to study the variation pattern of the central spike, it would seem a good working hypothesis to confine our attention to varieties which are without either condensation or multiplication. It is clear that condensation affects this part of the tassel but it produces such thickly set spikelets that all other variation is obscured. To understand the basic variables one must concentrate upon non-teratological strains; in other words, upon maize which is without either condensation or multiplication.

VARIATION IN NON-TERATOLOGICAL MAIZE

If in this way we exclude the effects of condensation and multiplication, variation in the central spike is simple. All of the maize we have examined then falls in two extreme classes and intermediates between them. The 8-rowed varieties have the spikelet pairs of their central spikes in whorls of two. The 12-

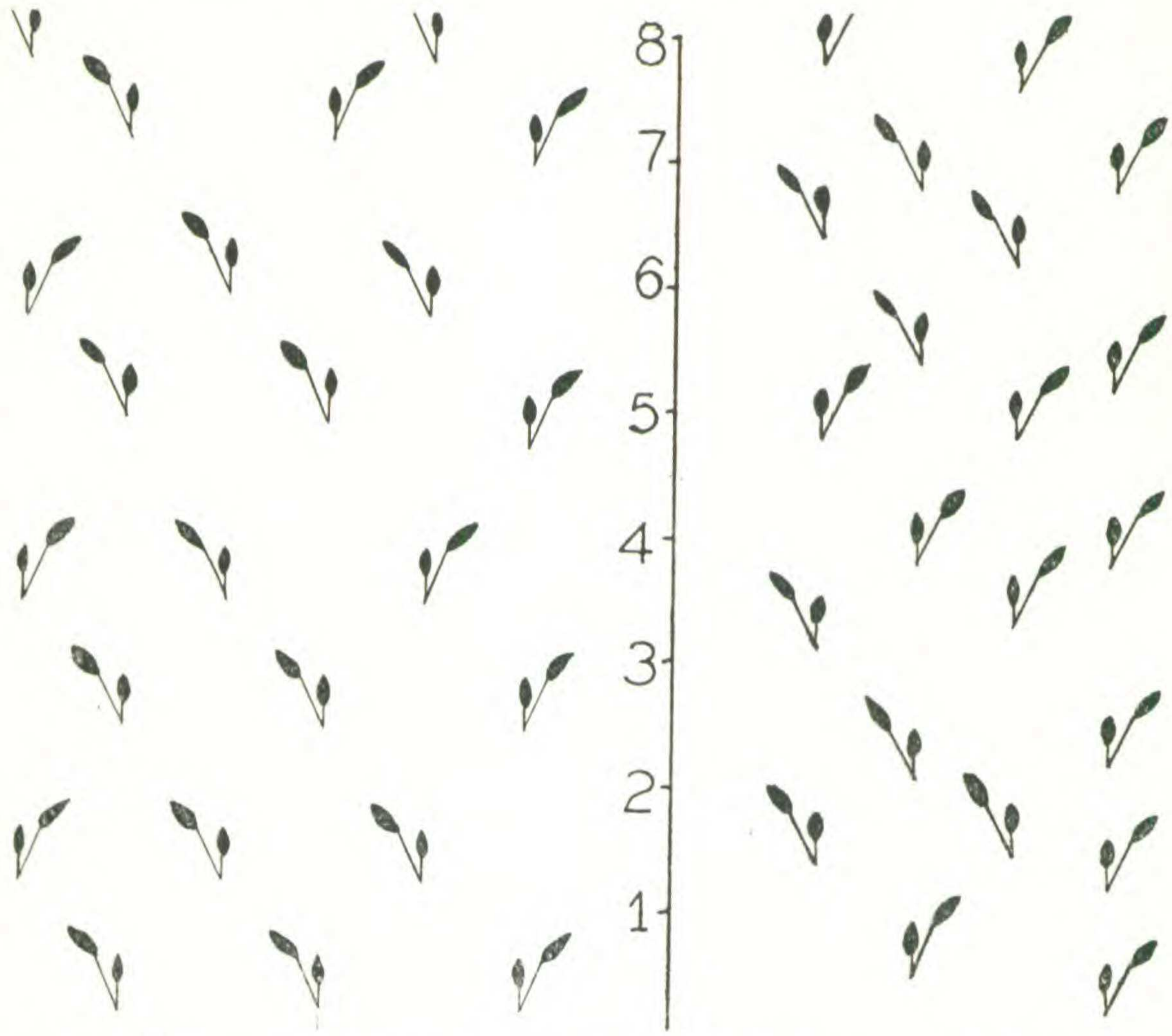

Fig. 4. Measured diagram showing spikelet arrangement in 8-cm. portions of two central spikes. Left, from a 12-rowed flour corn from the Southwest. Right, from an 8-rowed northern flint. Scale in cms. Further explanation in the text.

rowed varieties have their spikelet pairs in whorls of three. In the 8-rowed varieties, as for instance in the older varieties of flints of the northern United States, the spikelet pairs are opposite and decussate. That is, if the pairs at any one node are set east and west, those at the next node are north and south, then the next pairs east and west, etc. Looking down the spike from the apex there will be spikelet pairs on four sides of the central spike, making 8 rows in all. The 8-rowed ear has an 8-rowed central spike.

Similarly in 12-rowed varieties without condensation or multiplication, if the whorl of 3 pairs at any one node is represented by positions 2, 6 and 10 on the face of a clock, then at the next node we shall find positions 12, 4 and 8, then 2, 6, 10 again, and so on. Looking down the central spike from the apex we shall see spikelet pairs on six of its sides, making 12 rows of spikelets. The plant with a 12-rowed ear has a 12-rowed central spike to its tassel. The complete homology between the two organs is as simple as that. Figures 4 to 6 show spikelet positions as actually measured on representative central spikes. The measuring was done according to the method originated by Mangelsdorf (1945) but the results have been plotted on a scale of approximately equal value horizontally as well as vertically. The central spikes were examined under a dissecting microscope with a wide field. Accuracy was increased by having an assistant record the measurements. Several centimeters of the spike (usually a half to a third of its entire length) were chosen for examination. A mark is made with dye or ink at the precise spot where the measurements begin. The distance from each spikelet pair to this base line is recorded in millimeters, using a steel rule or calipers. Any one of the pairs at the base is chosen to begin with, and all the pairs which are on the same side of the spike are recorded in succession up the spike, removing each pair as it is measured. In some varieties there are ridges on the rachis which make it a simple matter to follow any one rank of the spike. In others the relationship is obscured, and one has more or less arbitrarily to choose a line of spikelet pairs. These pairs are then plotted to scale on cross-ruled paper, and successive vertical ranks to the right and the left of the original rank are measured until no spikelets remain on the portion of the spike chosen for study. The resulting graph is essentially a cylinder which has been cut down one side and flattened out into one plane. In attempting to make such an examination it is best not to begin with the more complicated types. An 8-rowed sweet corn or a northeastern flint will demonstrate how simple the arrangement can be and experience with it will aid one in interpreting the more complicated spikes of the dent corns.

Figure 4 demonstrates that, in the strict sense of the word, the arrangement of the spikelet pairs on the central spike is not in spirals as has been so frequently reported (as, for instance, in our own earlier papers on the subject). The pairs are clearly in whorls. In 8-rowed varieties they are in whorls of two, in 12-rowed varieties in whorls of three. In both of these sorts there is a regular alternation of whorl position so that the spikelet pairs can be followed in regular spirals in either direction, but this is not a spiral arrangement in the strictest sense. It is condensation which has obscured the simplicity of this regular whorling. With a low degree of condensation the whorling can still be made out from the scaled diagram though it is often difficult to determine from inspection. With a higher degree of condensation, the spikelet pairs are so thickly set upon the central spike that it is difficult or impossible, even from the diagram, to determine what the fundamental pattern may have been.

THE DETERMINANTS OF ROW NUMBER IN THE MAIZE OF THE UNITED STATES

Condensation and number of spikelet pairs per whorl are therefore the two main variables which determine row number in the maize of the United States. Multiplication, particularly in its lower grades, is occasionally met with, but it plays nowhere near the role it does in Guatemala or in South America. Since it may lead to irregular rowing and since the commercial varieties of the United States have been very strongly selected for straight rows, it is possible that its frequency may have been greatly reduced by this intense selection.

Figure 5 demonstrates how number of spikelet pairs per whorl and condensation interact in determining row number in the maize of the United States. Condensation is diagrammed on the vertical axis from the grade of 1.0, where there is no condensation and there is merely the normal pair of spikelets at each node, to the grade of 3.0, where there are on the average three spikelet pairs at each node. The horizontal axis shows the fundamental whorling of the central spike (and therefore of the ear as well) from whorls of two pairs at each node through various intermediate stages to whorls of three at every node. The numbers on the Cartesian surface show the row numbers to be expected with various combinations of these two tendencies.

For the interpretation of row number and particularly for its genetic analysis the most important fact demonstrated in fig. 5 is that for row numbers above 8 there are two quite different kinds of plants which can yield any row number. Take 12 rows, for example. They are to be expected on a plant with no condensation and with a central spike in whorls of three. They are equally likely on a

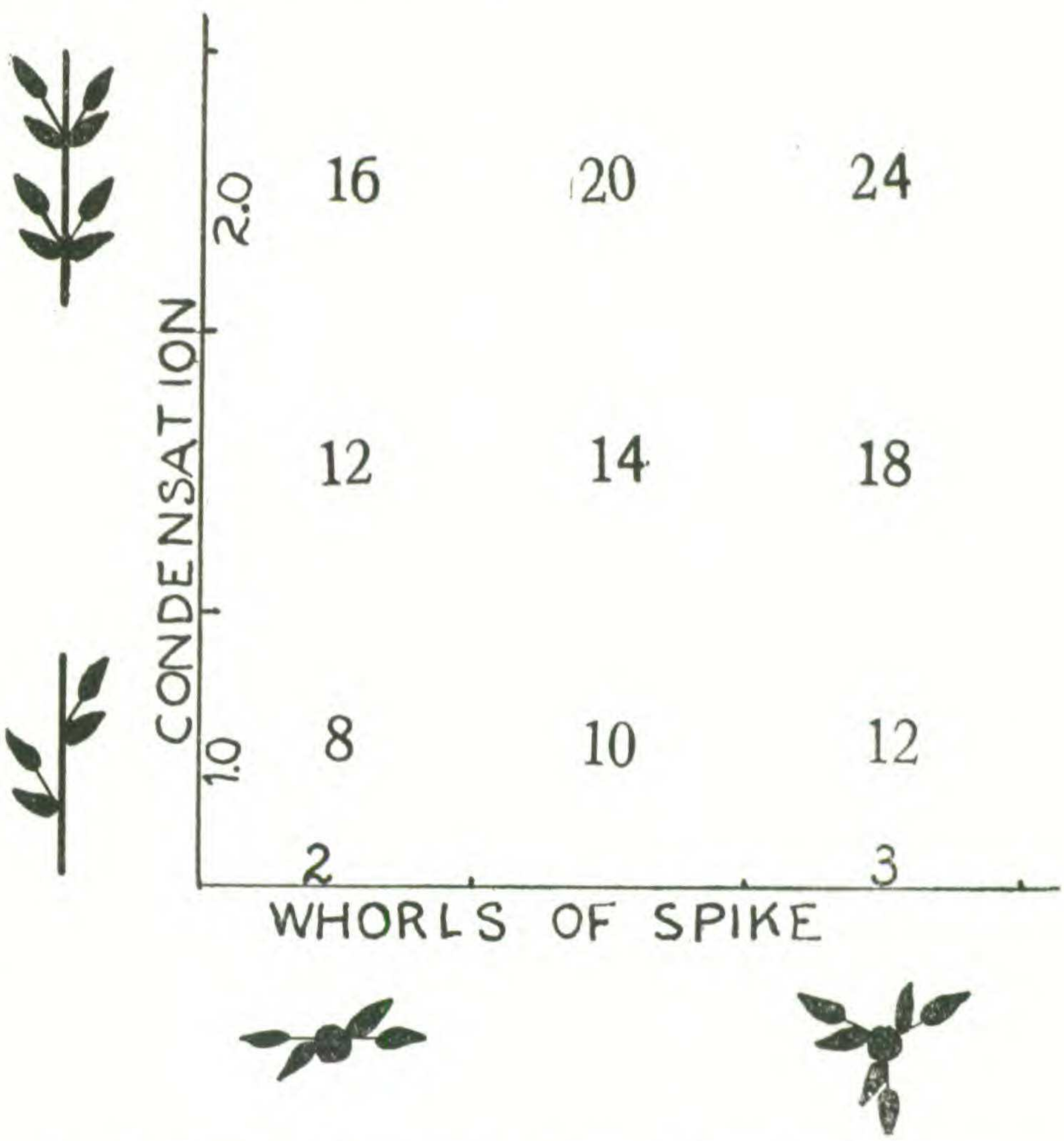

Fig. 5. Diagram showing how whorling and condensation interact in affecting row number. Whorling, from whorls of 2 pairs to whorls of 3 shown on the horizontal axis. Condensation from 1.0 to 2.0 shown on vertical axis. Numbers in the center show row numbers to be expected in the absence of modifying factors or other phenomena such as multiplication.

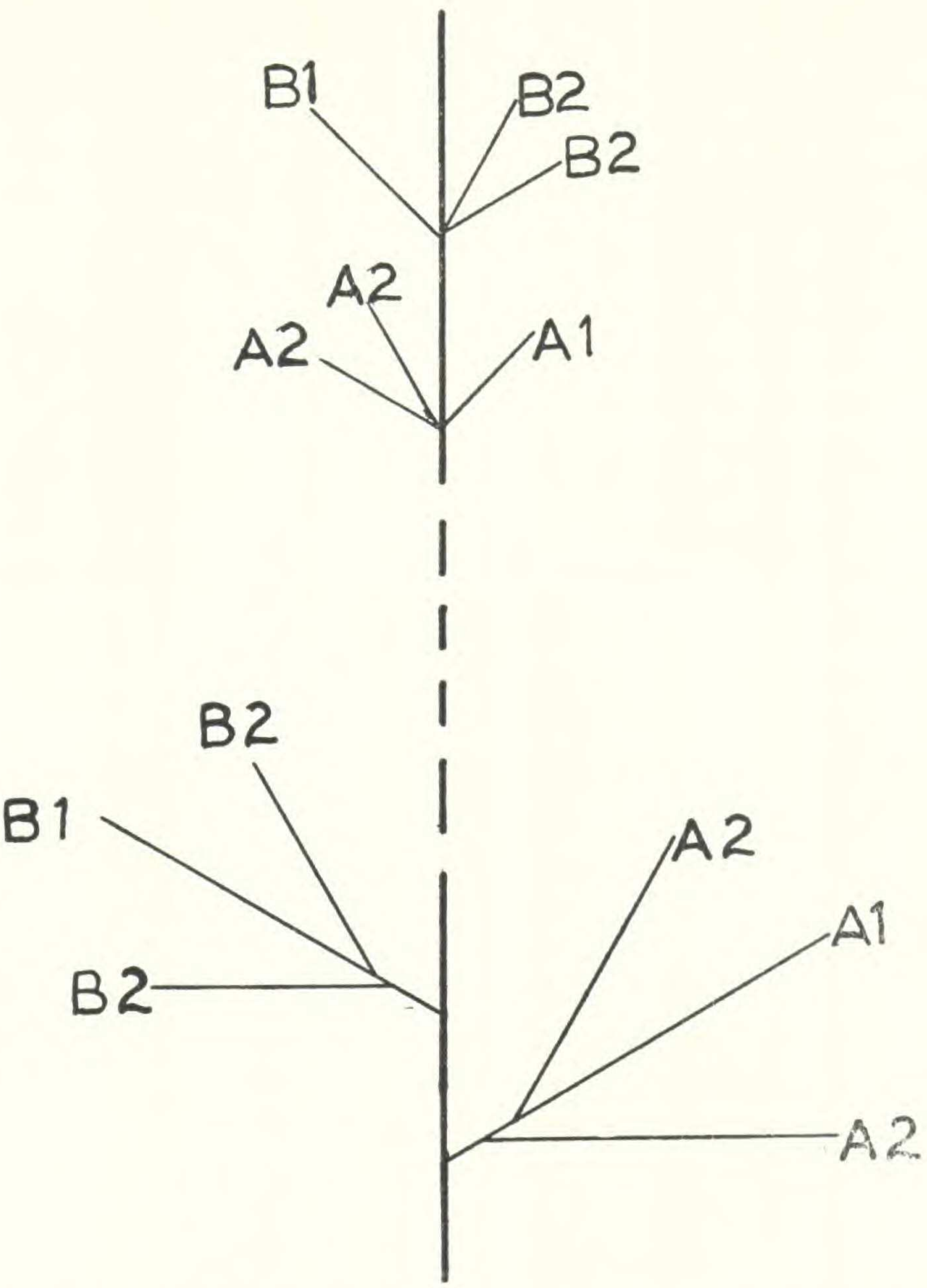

Fig. 6. Diagram illustrating possible relationship between the distichously arranged lower branches of a maize tassel and the whorled upper branches and central spike. Two lower branches are shown, each with its own axillary branches. At the upper nodes two such branches would be represented by two whorls of three. Each whorl takes the place of a primary branch and its two axillaries.

plant with whorls of two but with condensation of grade 1.5. Furthermore, these two types could be distinguished by examining their tassels. In the first type the arrangement of spikelets would be regular throughout, and the central spike would be in whorls of three. In the second type about half the nodes on the lowest secondary branch would have an extra pair of spikelets. The whorls of the central spike would be in two's, somewhat obscured by the disturbance of the spikelet pattern brought about by condensation.

THE INHERITANCE OF ROW NUMBER

The completion of the morphological analysis outlined above makes it possible to proceed with the genetic analysis of differences in row number. It demonstrates, however, the futility of attempting to study the genetics of row number as such. We must instead consider the genetics of condensation *and* whorl number *and* multiplication. Genetic investigations along these lines are already under way. The results now available, though not precise, suggest the general nature of the genetic background. Condensation is apparently due to one or two recessive genes with a considerable number of factors modifying its expression. Differences in whorl number are apparently due to at least several genes; the problem is a complex one. In an 8-rowed variety or in a 12-rowed variety the correspondence between whorl numbers in the tassel and in the ear are absolute. In crosses between such varieties, thresholds of expression may differ in different parts of the tassel and between the tassel and the ear.

THE BEARING OF THESE EXPERIMENTS UPON THE GENETIC ANALYSIS OF MULTIPLE-FACTOR CHARACTERS

Few branches of genetics are of more practical or theoretical significance than those which deal with the inheritance of multiple-factor characters. Yet in this field of genetics little fundamental advance has been made since East first demonstrated that the problem could be brought in line with a single-factor analysis. Row number in maize is such a problem. As the above analysis shows it cannot be understood genetically until it is understood morphologically. Now that we understand something about the morphological and physiological apparatus by which increases in row number are achieved, we are ready to plan a genetic experiment in which the number and distribution of genes responsible for row number differences may be determined, at least approximately.

To work effectively in such problems, one must, in other words, precede genetic analysis with morphological analysis. In a problem of this complexity, the morphological analysis is in itself a subject for research. This is equally true in most other investigations of multiple-factor characters. The general neglect of the morphological bases of such characters is one of the reasons the subject has progressed so little in the last thirty years.

THE ANATOMICAL INTERPRETATION OF THE EAR AND TASSEL

The inflorescences of *Zea Mays* have proved notoriously difficult to explain in terms of classical morphology. Weatherwax (1935) has pointed out that they share with certain other grasses a tendency to be whorled rather than distichous. That does not, however, solve the fundamental difficulty in interpretation. Why should the lower branches of a maize tassel be distichous and the upper branches spiraled or whorled? The facts reported above suggest an explanation. If we confine our attention to non-teratological inflorescences, the typical tassel has distichously arranged branches at its base, then passes through a zone difficult to interpret exactly and has whorls of spikelet pairs all along its upper portion.

Furthermore, these whorls alternate in an exact fashion between two clearly opposite types. If the whorls are of two pairs, for instance, the arrangement is decussate. The distichous branches at the base and the alternation of oppositely arranged whorls at the apex suggest that the tassel is fundamentally distichous throughout and that in the upper part of the tassel each branch has been reduced to a whorl of two or three spikelet pairs as the case may be. The intermediate zone would then be the region in which the reduction of a tassel branch to a whorl of branches has been only partially accomplished.

One argument in favor of this interpretation is that the uppermost tassel branches, those just below the central spike, are themselves clearly whorled, usually for one node and sometimes for two or more. On the view expressed above each of these whorls of two or three branches would represent one branch with its own branchlets condensed upon the main axis, as illustrated in fig. 6. Whorls of two would represent a branch with one branchlet, whorls of three a branch with two. It is perhaps significant that the northern flint corns which are almost universally decussate in their central spikes are also characterized by lower branches which have but a single branchlet.

SUMMARY

1. The problem of row number in maize was studied in the tassel as well as in the ear, the former organ being more accessible for study and its variation being more readily interpreted.

2. One of the chief variables in maize is "condensation," a telescoping of successive internodes. It operates throughout the tassel and the ear but is most effectively measured in the lowermost secondary branch of the tassel. When precisely scored it is directly related to row number by the equation $C = 10\ R$. In United States maize this relationship is less exact above 20 rows, probably due to the intensive selection against varieties with more than that row number during the corn show era.

3. If we rule out those varieties of maize with condensation and multiplication as being teratological abnormalities, then all the remaining varieties have central spikes (and ears) with spikelets in whorls rather than in spirals as has been so frequently reported. Eight-rowed varieties such as the northern flints are in whorls of two; 12-rowed varieties are in whorls of three.

4. The genetics of row number is therefore most effectively studied not as the genetics of row number as such, but as the genetics of condensation, multiplication, and whorl number. Preliminary results indicate that condensation is a simple recessive and that the genetics of whorl number differences is complex.

5. Two problems are discussed in the light of these results: The genetics of multiple-factor characters, and the anatomical interpretation of the ear and tassel.

LITERATURE CITED

Anderson, Edgar (1944). Homologies of the ear and tassel in *Zea Mays.* Ann. Mo. Bot. Gard. 31:325–342.

————, (1946). Maize in Mexico, A preliminary survey. *Ibid.* 33:147–247.

————, and Hugh C. Cutler (1942). Races of *Zea Mays:* I. Their recognition and classification. *Ibid.* 29:69–88.

Bonnett, O. T. (1940). Development of the staminate and pistillate inflorescences of sweet corn. Jour. Agr. Res. 60:25–37.

Carter, George F., and Edgar Anderson (1945). A preliminary survey of maize in the southwestern United States. Ann. Mo. Bot. Gard. 32:297–322.

Collins, G. N. (1919). Structure of the maize ear as indicated in Zea-Euchlaena hybrids. Jour. Agr. Res. 17:127–135.

Cutler, Hugh C. (1946). Races of maize in South America. Harvard Univ., Bot. Mus. Leafl. 12:257–291.

Emerson, R. A., and E. M. East (1913). The inheritance of quantitative characters in maize. Res. Bull. Nebr. Agr. Exp. Sta. 2.

Lindstrom, E W. (1929). Linkage of qualitative and quantitative genes in maize. Amer. Nat. 63:317–327.

————, (1931). Genetic tests for linkage between row number genes and certain qualitative genes in maize. Iowa State Coll., Res. Bull. 142, pp. 250–288.

Mangelsdorf, Paul C. (1945). The origin and nature of the ear of maize. Harvard Univ., Bot. Mus. Leafl. 12:33–75.

Weatherwax, P. (1916). Morphology of the flowers of *Zea Mays.* Bull. Torrey Bot. Club 43:127–144.

————, (1917). The development of the spikelets of *Zea Mays. Ibid.* 44:483–496.

————, (1935). The phylogeny of *Zea Mays.* Amer. Midl. Nat. 16:1–71.

Wellhausen, E. J., L. M. Roberts, and Lee W. Lenz (In press). Relation between tassel condensation and ear row number in maize.